

XVII. *On a lepidopterous pupa (Micropteryx purpurella) with functionally active mandibles.* By Dr. THOMAS ALGERNON CHAPMAN, M.D., F.E.S.

[Read May 10th, 1893.]

THIRTY years ago Mr. Stainton exhibited the pupa of *Micropteryx (purpurella?)* to this Society, and figured it in the 'Entomologist's Annual.' His description of it is very good, and I believe absolutely correct so far as it goes. The paragraph that is most vague says:—"Below the eyes and above the palpi appears a brown knob, which may possibly represent the tongue; it bears numerous bristles; immediately beneath it are two large brown projections, the use of which I am utterly at a loss to conjecture; they expand towards the tips, which are scalloped obliquely."

Since this date nothing of importance has appeared on the subject, so far as I can ascertain. Mr. Charles Healy describes the emergence in the 'Entomologist's Monthly Magazine,' first number, p. 20; yet, though a minute and careful observer, he appears to have failed to note the use of the jaws in emergence, and no doubt many entomologists have made observations such as my friend Dr. Wood has often repeated to me, that the empty pupa-case lies on the surface of the soil after the moth has emerged, and is a curious bit of shrivelled membrane not at all like a pupa-case. But no one appears to have arrived at the surely very obvious conclusion, that the "two large brown projections" of Stainton are the mandibles, still less to have observed the use made of them by the pupa.

That a lepidopterous pupa should have jaws, in other than the obsolete form in which all (?) lepidopterous pupæ have them, is remarkable enough. That they should be of such immense size proportionately to the insect, and should be functionally active, seems at first sight incredible, though the still more remarkable fact

remains, that active and powerful as they are, there are no visible means of working them, as they are pupal structures, used only immediately before the emergence of the imago, and have no corresponding imaginal parts attached to them. Yet all this may be easily observed by anyone who will get the necessary material,—by no means difficult to do,—and take the trouble to watch it from 6 to 7 a.m.

The pupa has all its appendages apparently quite separate and unfused together in any way, and the abdomen is thus not only unattached to legs and wings, but preserves freedom of movement in all its segments. The head and thoracic segments are equally free to move on each other, and do so, especially the head, during emergence. Yet, when the pupa is quiescent, *i. e.*, removed from its cocoon some time before emergence, it does not move these segments when irritated, but only the abdominal ones.

The toughness and density of the cocoon, and the great delicacy of the pupal skin, are remarkable, and probably bear such a relationship to each other that the one may be said to compensate for the other. The only portions of the pupa-skin at all solid are the labrum (Stainton's brown knob), which carries six long hairs on either side, and the jaws and an oval hoop, to which they are articulated.

The front of the head carries two long hairs on either side (the antenna-basal hairs that occur throughout so large (all?) a number of Heterocerous pupæ). The antennæ cross the prothorax in a free loop, and pass downwards into the usual position between the wings and legs, but being quite unfixed or fixed by mere contact, and not by fusion of surface even in the slightest degree, it happens (as Stainton found in his specimens) that one or both antenna have not unfrequently a position on the wing or over the legs.

The brown knob or labrum, with its six long bristles on either side, is a large solid piece, containing no imaginal structure, but doubtless serving by its hairs as a tactile organ during the exit of the pupa, and by its solidity assisting the action of the jaws, probably both as a solid base to act from and as attaching the parts to the imago. Beneath these are the jaws, great curved organs, proceeding first directly forwards, then by a

sweep of a quarter of a circle becoming directed to the other side, and, crossing the jaw of the other side, proceeding transversely till the extremity projects rather beyond the margin of the opposite side of the pupa; the shaft is enlarged at either end, proximally with three projections or knobs for articulation; at the other end into a large truncate knob, the margins of whose flat extremity are armed with three or four large teeth, and many smaller ones, reminding one in appearance, as they certainly resemble in function, the fore paws of a *Gryllotalpa* or *Cicada* pupa. The inner margin of the shaft is armed by a row of nine or ten teeth, flat, sharp, and leaflet-like.

The maxillæ are very inconspicuous, but carry the very large maxillary palpi, which pass directly outwards transversely to the margin of the pupa, and then return to the centre line, the returning portion ventral, and perhaps a little posterior to the outward half. It appears to be quite free throughout its length, but is not moved during pupal existence. The position is the same as in Heterocerous pupæ that possess it, but in them it is closed in by the neighbouring parts, except the front of the terminal segments.

The labial palpi are large organs, passing forwards when the head is raised at an angle to each other of 70° or 80° , and reaching quite in front of the jaws (when closed), and used apparently as tactile agents during emergence; but that they actually possess any freedom of movement of their own, I am not inclined to believe.

The legs and wings lie in much the usual positions that these parts occupy in other pupæ, but with the less definiteness due to the fact that they are not fused together, and any of them may be lifted away from the others, though the insect itself is unable to do so, except during emergence, when certain distortions, due to the partial withdrawal of the parts, occur.

The side of each abdominal segment has a long hair, nearly as long as the diameter of the pupa, and there are shorter ones dorsally.

When the pupa is ready for emergence, the head of the imago, the chitinous plates of the thorax, and the legs and wings, become black. The plates of the abdomen remain nearly colourless, as do the membranes between the thoracic plates. It is worthy of note that the

1st abdominal segment in this matter declares itself to be truly a 4th thoracic segment, presenting similar chitinous plates to those on the 3rd thoracic, though rather smaller, and with more intermediate membrane, and not at all like the simple colourless plate of the 2nd and following abdominal segments.

The oval hoop that carries the jaws, and is so obvious in the cast pupa-skin, is not very evident before emergence; it appears to have several oblique bars, but its actual form is difficult to fully grasp, and without figures hopeless to describe to any purpose.

It may be well to mention that *purpurella* only spends some five or six weeks above ground as imago, ovum, and larva; the rest of the year is spent buried in the soil, chiefly as a resting larva, and for a few weeks as a pupa. To insure its safety, it buries itself deeply, and spins a cocoon of remarkable strength for so small an insect. The depth is probably usually $\frac{1}{2}$ in. to 2 in., but 8 in. to 10 in. are reported by persons who have reared them, but probably supplied them with light open soil; this is proportionally as though, say *Acherontia atropos*, were to go down 15 or 20 ft. It is to enable it to escape from this hard cocoon and the superincumbent earth that the active jaws come into use.

I ought not to omit to state the comparative size of the mandibles, which is great, so as to be comparable with, say, those of *Lucanus cervus* ♂, rather than with those of any lepidopterous larva; the length of the pupa is about 4 mm., its greatest width about 1·3, the width of the head about 0·9, whilst the length of each mandible is about 0·7 mm.

When in the cocoon the empty larva-skin is tucked away under the extremities of the leg and wing-cases, and between them and the abdominal segments. In the curved attitude of the pupa in the cocoon there is certainly more room for it here than elsewhere, and so it probably gets here rather readily by the movements of the pupa.

Micropteryx purpurella emerges about 6 to 7 a.m., and on the mornings of March 10th, 11th, and 12th, and on several occasions afterwards, I had the pleasure of observing some specimens do so. I had sorted out the cocoons from the sand in which they had been made, and had them lying loose in a jar on the surface of some

damp sand. The first thing to be seen was some movement at one end of the little cocoon, and on picking it out and observing it through a glass, though they are not so small as to prevent a good deal being seen without artificial aid, there is observed to be a rather ragged hole in the end of the cocoon, and the jaws of the pupa are seen actively opening and closing; by the time the cocoon is spotted and taken out, the opening of the cocoon is practically finished, and the head of the pupa very shortly emerges. The pupa now rests a little, and then again elevates the head and works the jaws, the object being in all probability one that is, under the circumstances, unnecessary, *viz.*, to make its way through the earth above the cocoon. In raising the head the face is lifted right away from the front of the pupa, and is directed very much forward, and moves from side to side with both an angular and rotatory movement, and seems indeed to be as free to move as the head of a *Carabus* or an earwig; the jaws work to and fro, opening till they can pass each other and shutting again, sometimes with the right one in front of the left, sometimes with the left in front. The maxillary palpi lie just behind them, folded back closely, quite inert, in the ordinary position they occupy in the "incomplete" pupa; but the labial palpi are strongly protracted, and perhaps move to some extent, and seem at least to be in active use, no doubt to guide the action of the jaws in some degree. The long hairs of the vertex and labrum are also, no doubt, of much use for this purpose.

Following, or rather along with, this action of the head and jaws, the pupa further protrudes from the cocoon, the next stage setting free the prothoracic or first pair of legs, that is, the pupa is half out of the cocoon and the first pair of legs are clear of it to their extremities, and it is now seen that they are not adherent to any other part of the pupa; the prothorax, with its legs, being freely movable on the head at one side, and on the mesothorax on the other, but the legs are fixed in their own cases, in the flexed attitude common to pupal legs, and do not move either in their own joints or on the prothorax. It results, that the stiff and imprisoned legs, in some of the movements, are raised to an angle of 90° from their position of pupal rest, and instead of resting down against the other appendages,

are pointed directly forwards. In the movements of the head it is now seen that the antennæ form a great free loop across the prothorax, and are indeed but slightly attached to the wings, and some become free there also, forming no impediment whatever to the movements of the head. In different individuals there is a variety as to whether the pupa shall rest here for its further emergence, a few doing so; a further, rather larger, number progress a little more, and emerge with a few abdominal segments still within the cocoon, but the majority free themselves entirely from the cocoon before progressing any more. Still, the movement by which they leave the cocoon is much the same in character, if not, indeed, the actual exertion, by which the moth emerges from the pupa-case, which up to the present is unbroken. At this point again a rest is often taken, the rests corresponding, no doubt, with the emergence of the pupa, first from its cocoon, and secondly from the overlying earth.

The pupa is now, in most instances, in full view, and one recognises at once that the movements that are now taking place, and those we have so far been watching, are very unlike those we are used to in seeing a moth or butterfly emerge from the pupa, not so much in themselves as in the participation in them of the pupal skin, and resemble much more the moulting of a larval skin, the pupal skin partaking of the movement of the contained moth as the larval skin does, and even the 2nd and 3rd thoracic segments bearing the wings have a certain amount of movement on each other. The prothoracic pupal skin becomes widely stretched as the movements of the moth forces a larger bulk into the head, and the first legs show the front of the pupa to be stretched, and they take up the porrected attitude already described. In the meantime the abdomen has been progressing in its pupal skin, which is here very flimsy, the tracheæ are seen drawn out of the spiracles, and passing forwards from the spiracles of the pupal skin to those of the moth, and a portion of pupal skin is empty and shrivelled at the anal extremity.

The pupal skin now splits down the back of the thorax, sundry long thoracic hairs protruding. Except the head, wings, legs, and some thoracic plates, the moth is still white and colourless, and the hairs clothing the

abdomen, though dark, seem very sparse. The splitting of the pupa allows the head and 1st thoracic segment very shortly to assume a more normal attitude, but during this period the prothorax of the moth is stretched so as to show its still very larval structure, *viz.*, it is largely white, colourless membrane, the spiracle with the tracheæ drawing out of it is very distinct, close to this is a not much larger rounded tubercle (supra spiracular ?), carrying a bundle of long hairs, and dorsally a narrow plate (as usual on larvæ), also carrying long hairs.

The splitting of the pupa-case takes place along the dorsum of the 1st and 2nd thoracic segments, and slightly encroaches on the head ; it does not, however, affect the 3rd thoracic segment, nor apparently does any lateral branching of the opening occur. The curious sausage-like rolls of the 3rd and 4th (1st abdominal) thoracic segments lie flattened and empty, as does also the curious wattle of similar structure that projects over the face. My first idea of the use of these, that they formed a sort of elastic cushion or base, by which the pressure necessary to open the cocoon was conveyed, protecting the moth to some extent from it, seems therefore to be unfounded. As soon as the real emergence of the moth from the pupa begins, and the first indication of this is the sliding of the abdominal pupal pellicle backwards, all movement of the jaws ceases.

The emergence of the moth takes place by the usual vermicular movements. When it has partially occurred the legs, being actually quite free from each other, look curiously dislocated, the pupal legs (or rather leg-cases) being displaced by the partially extracted imaginal legs. The expansion of the wings takes place *pari passu* with the emergence, and it often happens that the wings are fully expanded, except their extreme tips, whilst these tips are still included in the pupal wing-cases ; and whilst it seems to be normal for the wings to be freed before the abdomen completely escapes from the pupa, it often happens that the abdomen is first free, and is then curled round and used to shove off the pupal case from the wings. As soon as the moth is free from the pupal skin, the wings are practically fully expanded, but the moth crawls to a position suitable for hanging its wings backwards, as moths do as soon as the wings

are expanded, and this it immediately does for a brief period.

In working the jaws, the pupa moves its head up and down to the right and to the left, and with also some oblique twisting motion; the action of the jaws suggests some energy. Their movements and their size relative to the pupa might be illustrated by likening them to a man's arm crossed over his chest, as their position of rest, and (the elbows being stiff) the arms are then to be opened till they can be crossed again with the upper one undermost, very much the movement of a cabman warming his fingers, though less rapid. The hands are not relatively large enough to represent the expanded digging extremities of the jaws, whilst the fingers are too long for the teeth with which they are armed; so that the illustration must not be pushed too much into detail.

When the pupa is reposing after breaking through the cocoon, the lightest touch by a needle-point either of the jaws, the labial palpi, or the long hairs of the head or labrum, at once causes them to work, one might say most intelligently, with the obvious object of breaking down some impediment in front, the head reaching in turn as far forwards and as far to either side as possible. I ought to note that of the points arming the end of the jaw, one, the largest, is quite curved into hook form, pointing backwards, and seems specially designed for gripping and tearing the cocoon.

How are these jaws worked? They and the corneous labrum in front of them are empty of any imaginal parts, and with the corneous ring-like base to which they are articulated, they are cast with the pupal skin a few minutes after they have been used; nor does the imaginal head contain any muscles adequate to move them with the force they display; nor does it present anything I can recognise as jaws, though there are some papillæ that probably represent them.

In the imago examined as soon as the head is free, there is a white smooth area above the maxillæ and between the eyes, which becomes afterwards darker and difficult to find, and, I believe, becomes smaller. This area is therefore probably expanded during emergence, much as the forehead of some *Muscidæ* is (*Musca*, *Exorista*, &c.), and I can imagine no way in which the

jaws can be worked than by fluid pressure acting in some way on their bases or on their contents, either by the contraction and expansion of this area, or of fluid acting through the mouth and imprisoned by the pressure of this area against the chitinous ring.

Walter (*Jenaische Zeitschrift*, 1885, p. 760) describes certain chitinous ridges as representing the jaws in the imago of *Micropteryx*, partly led thereto by the analogy of *Eriocephala*, and partly, no doubt, by the fact that a chitinous ridge in this situation is a jaw, if it is any true mouth-part; and I am not prepared to say that he is in error in doing so; whilst my own observations were not made with sufficient accuracy, owing, I think, as much to my own inexperience in such matters as to the inherent difficulties attending them; but it appeared to me that these chitinous ridges were rather borders to the pale soft area already referred to, and formed a margin into which the hard ring carrying the jaws was fitted.

The whole question, however, of how these jaws are worked will form an interesting research for some micro-anatomist. I fear my own training leaves me unequal to carrying the matter much farther. I am, however, thoroughly satisfied on two points—1st, that there are no muscles attached to these jaws; 2nd, that there are no imaginal jaws within them, whose movements compel those of the pupal ones.

If we are to accept, as I suppose we must, these creatures as veritable Lepidoptera, then the whole character of the pupa, as especially displayed in the emergence of the moth and the character of the moth itself at that epoch, are only slightly less remarkable than is the possession of active jaws.

The pupal case, except portions of the head, and the wing and leg cases, is very soft and delicate, and shrivels up as the moth emerges, much as a larval skin does; no joint even of the limbs seems quite soldered, but those of the segmental incisions are quite as freely movable as in a larva, and the intersegmental membrane is, notably on the prothorax, stretched by the moth inside pressing forwards, just as a larval skin is; and similarly the first indication that emergence has made any progress is the appearance of some shrivelled empty pupal skin at the anal extremity, and the shrivelling up

of the whole pupa-case after the moth has emerged, as well as the splitting for dehiscence being only one dorsal slit, are quite parallel with larval ecdysis, not with pupal, anywhere else in Lepidoptera to which my knowledge extends. The moth itself also, as regards much of the integument, especially the chitinous plates of the abdomen, is white and colourless till after emergence. In all these respects the analogy is much closer with Coleoptera than with the mass of Lepidoptera.

I must call attention to an error of nomenclature into which I have fallen, having applied the names *Micropteryx* and *Eriocephala* in precisely the reverse way to their proper meanings. *Micropteryx* is the name for the subject of these remarks—*purpurella*, and the *purpurella* group, the “Higher” *Micropteryges* of Walter and others—the tree-feeders, leaf-miners, and leaf-piercers—jawless as imagines, but not as pupæ. *Eriocephala* is the name for the *Calthella* group, the “Lower” *Micropteryges* of Walter—the pollen eaters, with simple ovipositors and active jaws (as imagines); the larvæ moss-feeders, with twenty-two legs. The names are so applied in Stainton’s monograph.

I may here call attention to an error into which I fell in my recent paper on pupa, *viz.*, as to the pupæ of *Pyrales*. I stated these to be without maxillary palpi; I find, however, that they exist in not a few *Pyrale* pupæ; and further, that of the non-Macro section of the *Obtectæ* most groups have one or more characters that are more developed in and more diagnostic of the *Incompletæ*; such as the possession of maxillary palpi, of a pre-prothoracic element, and even in having the glazed eye attached to this on dehiscence in rare instances.

I am indebted to my friends Mr. Bankes and Mr. Tutt for the information that the pupa of *Endromis versicolor* emerges from its cocoon before the escape of the moth. As Mr. Bankes hopes to further investigate this curious instance of an “Incomplete” habit resorted to by a Macro, I will content myself with this mere mention of the habit.

I notice also that Scudder states that the pupæ of the Sphingid genus *Macrosila* emerge from the earth for the escape of the moth, using for the purpose certain flanges in the spiracular region. These exceptions (by reversion?) require a modification of my statement that no

Macro pupa possesses this habit, though certain details, both of structure and habit, differentiate these cases of Macros from the ordinary habit of *Incompleteæ*. Mr. J. E. Robson also calls my attention to the habit of the pupa of *Lasiocampa rubi* of travelling up and down in its cocoon in order to make the most of available sunshine.

All these cases seem to me to be re-acquirements, by Macros that had long lost them, of the primæval habit of *Incompleteæ*.

I have observed in some Macros a structural point, giving strong confirmation to the idea that the Macros are a much younger form than the Micros. In some species the male pupa has a more marked incision between the 7th and 8th abdominal segments than the female has, even at times looking as if this articulation admitted of movement. This is never the case, but it appears to prove unquestionably an ancestry with the 7th segment "free" in the male to a later period than in the female.